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DESCRIPTION OF A NEW SUBGENUS (*ARBORIMUS*)  
OF *PHENACOMYS*, WITH A CONTRIBUTION  
TO KNOWLEDGE OF THE HABITS AND  
DISTRIBUTION OF *PHENACOMYS*  
*LONGICAUDUS* TRUE

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## A INTRODUCTION

Dr. C. Hart Merriam, in describing *Phenacomys albipes* (1901, p. 125), referred to *Phenacomys longicaudus* as being one of the rarest and least known mammals of the world. At that time only three specimens of *longicaudus* had been collected: the type, at Marshfield, Coos County, Oregon, an aberrant specimen at Meadows, Lane County, in the same state, and an example found dead on a road at Lierly's Ranch, near Mt. Sanhedrin, Mendocino County, California. The specimens from Oregon were transmitted to the United States National Museum by Aurelius Todd of Eugene; while the lone example from California, collected by A. S. Bunnell, was part of a collection which went to the Academy of Natural Sciences of Philadelphia.

The species first became formally known to science through the publication of the original description by True (November 15, 1890). For twenty-two years thereafter the species was represented in the museums of the United States by not more than the three specimens mentioned above.

According to Bailey (1915, p. 148) Dr. William Bebb of Los Angeles, in 1907, showed him several specimens of the tree mouse which he had taken at an Oregon lumber camp. "The men were chopping down tall Douglas spruces and he watched when the trees came down and caught several of the stunned or crippled mice as the nests were crushed by the fall."

In 1912 a specimen was secured by a game warden on the slope of Chaparral Mountain above Maple Creek Postoffice, Humboldt County, California, and turned over to Mr. C. I. Clay, of Eureka, who forwarded it to the Museum of Vertebrate Zoology of the University of California. The following year, through the activities of the California North Coast Counties Expedition sent out from the same Museum, sixteen specimens were collected at Mendocino City, Mendocino County, California, and one at Lierly's Ranch, four miles south of Mount Sanhedrin, in the same county. During the spring and fall of 1913, Mr. H. E. Wilder, of Carlotta, Humboldt County, California, collected and transmitted to the Museum of Vertebrate Zoology a series of thir-

teen specimens, one taken at Cuddeback, and twelve at Carlotta, Humboldt County. In February, 1914, Professor John F. Bovard and Mr. Alfred C. Shelton, of the University of Oregon, secured three more on Spencer Butte, seven miles south of Eugene, Oregon; and in June of the same year Mr. Vernon Bailey, of the Bureau of Biological Survey of the United States Department of Agriculture, collected an additional specimen in the same locality.

During these later years other specimens, of which the present writer has no record, may well have been collected; for the species is fairly abundant and widely distributed in certain sections of the humid coast belt, and its meager representation in collections is obviously to be accounted for through ignorance of its habits rather than any actual rarity.

Doubtless a few residents in localities where the species occurs have long known of its existence. Our attention, while working at Mendocino City, was first called to it by small boys. In a letter to the writer Mr. Wilder states that middle-aged men have told him of getting these "red mice" around the school house when they were pupils there.

The comparative recency of knowledge of *Phenacomys longicaudus* on the part of systematists, and the poverty of material representative of it, have had two effects, one beneficial, the other detrimental: The species has been preserved from the burden of synonymy which so involves all our more widely known species, it never, in fact, having been known by any other name than the one which it bears at present; and it has previous to the present time been impossible to determine with any definiteness the systematic and ecologic status of the species. This paper aims to be a contribution to the latter problem.

It should perhaps be here noted that the name "lemming-mouse," which has been applied to *Phenacomys*, is not strictly correct. For this name should be reserved for the members of the supergeneric group of the *Lemmi*, which includes *Synaptomys*, *Dicrostonyx* and *Lemmus*. On the other hand *Phenacomys* belongs to the supergeneric group of the *Microti*, or voles, which includes also *Fiber*, *Evotomys* and *Microtus* (see Miller, 1896, p. 8).

As regards their habits the *Microtinæ* are notably adaptable. The situations in which they are found are many and varied. They are encountered “. . . from sea beaches to marshes and Alpine mountain tops, and from open plains to the densest forests . . . . While the great majority of species spend much of their time on the surface, protected by the overhanging vegetation, a few live almost exclusively underground, and in consequence of this habit have acquired numerous modifications which fit them for the needs of a subterranean life. Others are amphibious and never occur at any great distance from water” (Miller, 1896, p. 10). Of all members of this great subfamily, *Phenacomys longicaudus* is unique in its choice of an arboreal habitat; and we may well inquire as to whether this peculiar habit may not be weighted as of importance in the classification of the species. The use of habit characters is not without precedent in the *Microtinæ*. Before the publication of De Selys Longchamps’ “Essai Monographique sur les Campagnoles des environs de Liege,” 1836, the voles had been divided into two groups according to their habits, the aquatic species being separated from those that are strictly terrestrial. But beginning with and subsequent to this author habits as characteristics of the organism appear to have been left out of count in the classifications of the group.

Miller (1896, p. 24) has clearly shown the impracticability of the subdivision of the genus *Microtus*, and the same holds with regard to the subfamily *Microtinæ*, according to the variations in any *one* set of characters, and in his own work bases the classification upon an assemblage of characters, all drawn from the province of *physical* peculiarities. Of these the following are regarded as the more important: form of skull, structure of bony palate, pattern of enamel folding, number of mammæ, number of plantar tubercles, and presence or absence of musk glands on the sides. Regarded as of lesser importance are: quality of fur, hairiness of soles, length of tail, form of front feet, size of eyes, and form of external ear.

It would appear that the greater the assemblage of characters on which a classification is based, so long as such characters are comparable in degree of constancy, the more ade-

quate the classification. In the present paper characters have been freely drawn from two important additional provinces, namely those of *geographical distribution* and of *habits*.

In general, characteristics from these provinces are not sufficiently well known to permit of their use to any great extent. Confessedly, also, such characters, especially those from habits, are often less tangible and far less convenient than physical characters, but as information is accumulated they must certainly find larger place in taxonomic considerations.

In view of the aberrant nature of *Phenacomys longicaudus* there would seem to be some argument for the erection of a new genus for its reception. It seems to the writer, however, that a principle given expression by several authors, notably Osgood (U. S. Dept. Agric., Bureau Biol. Surv., N. Amer. Fauna 28, 1909, pp. 24, 25), and Sumner (Science, June 18, 1915, pp. 899-902), should be recognized, namely, that in a classification which is inevitably critically analytic, the synthetic phase should not be forgotten. The multiplication of genera for the purpose of emphasizing group differences which are comparatively slight would seem to be unwise.

In the present instance, particularly, the chance that the fundamentally close relationship of *Phenacomys longicaudus* to the genus *Phenacomys* will be overlooked is greater than the chance that its differences therefrom will not be appreciated, so it has seemed wisest to accord it subgeneric rank only.

The chief characteristic of our knowledge of mammalian life-histories is its incompleteness. It is estimated that of even our best known species the life-history material available is only five to twenty-five per cent of what it should be. These considerations emphasize the obligation imposed upon the investigator to put on published record such facts regarding habits as he may discover.

While it is to be hoped that the study of morphology will be no less vigorously prosecuted in the future than in the past, it would seem desirable that the study of psychological predilections and associational relations be much more emphasized in the future than in the past. Habits and associa-

tional relations are just as much a part of the animal as are its physical characters. They are just as distinctive specifically; and there is no good reason why they should not be accorded just as full treatment.

## B MATERIAL AND ACKNOWLEDGMENTS

The following specimens constitute the material basis for this study:

*Phenacomys intermedius*—Total number, 3. Alberta, head of Smoky River, 2 (U. S. National Museum). British Columbia, South Fork Moose River, 4525 feet, 1 (U. S. National Museum).

*Phenacomys orophilus*—Total number, 17. Washington: Mt. Rainier, 5000 feet, 2 (U. S. National Museum). Montana: Bear Tooth Mountains, 1 (Biol. Surv. Coll.). Idaho: Sawtooth, 2; Salmon River Mountains, 1 (all from Biol. Surv. Coll.). Oregon: Lane County, Three Sisters Mountain, North Base, 5000 feet, 1 (Coll. Univ. Oreg. Mus. Dept. Zool.); Lane County, Three Sisters Mountain, N. W. slope, 7400 feet alt., 1 (Coll. Oregon Game Department); Crook County, Deschutes River, Mouth of Davis Creek, 1 (Coll. Oregon Game Department). California: Mt. Shasta, Squaw Creek, alt. 7800 feet, 2 (1, skull only); Mount Shasta, head of Squaw Creek, 1; Tuolumne Meadows, 2; Mt. Lyell, 2; Mono Pass, 1 (all from Biol. Surv. Coll.); Pyramid Park (= Peak), 1 (Coll. Field Mus. Nat. Hist.). Canada: Northwest Territory, Red Deer River, 1 (Coll. Field Mus. Nat. Hist.).

*Phenacomys albipes*—Total number, 2. Oregon: Lane County, 2 miles W. of Vida, 1 (Coll. Oregon Game Department). California: Humboldt Bay, Arcata (in redwoods), 1 (the type, Biol. Surv. Coll.).

*Phenacomys olympicus*—Total number, 9. Washington: Happy Lake, 8; Boulder Lake, 1 (all from Coll. Field Mus. Nat. Hist.).

*Phenacomys longicaudus*—Total number, 37. Oregon: Coos County, Marshfield, 1 (the type, U. S. National Museum); Lane County, Meadows, 1 (Biol. Surv. Coll.); Eugene, 4 (1 from Biol. Surv. Coll., 3 from Coll. Univ. Oreg. Mus.

Dept. Zool.). California: Humboldt County, Mad River, Big Bend, southeast from Kneeland, Chaparral Mountain, on slope above Maple Creek Post Office, 12; Carlotta, 12; Cuddeback, 1; Mendocino County, Mendocino City, 16 (4 in alcohol); Lierly's Ranch, 4 miles south of Mount Sanhedrin, 1 (all Coll. Mus. Vert. Zool. Univ. Calif.).

The writer desires to extend grateful and cordial acknowledgment to the following persons: For the loan of specimens, to Messrs. H. W. Henshaw and E. W. Nelson, of the Bureau of Biological Survey of the U. S. Department of Agriculture, to Messrs. Richard Rathbun and Gerrit S. Miller of the U. S. National Museum, to Mr. Wilfred H. Osgood, of the Field Museum of Natural History, to Mr. Alfred C. Shelton of the University of Oregon Museum, Department of Zoology, and to Mr. Stanley G. Jewett, of the Oregon Game Department; for identification of lichen used as nest material by the tree mouse, to Professor William A. Setchell, Professor of Botany, University of California; for microscopical examination of nest material to Dr. T. H. Goodspeed of the University of California; and for much valuable information as to the habits of the tree mouse to Mr. Alfred C. Shelton, of the University of Oregon, to Mr. C. I. Clay, of Eureka, California, to Professor Walter K. Fisher of Stanford University, and to Mr. H. E. Wilder, of Carlotta, Humboldt County, California. References in the text to Messrs. Shelton, Fisher, Clay and Wilder are on the basis of their correspondence with the writer. The success of the expedition sent out by the Museum of Vertebrate Zoology to the north coast counties of California, which collected material representative of *Phenacomys longicaudus* and much valuable information regarding its occurrence and habits, is in no small measure due to the following men, who accompanied the writer, and whose enthusiastic co-operation made the work a pleasure: Mr. Gordon F. Ferris, of Stanford University; Mr. Charles L. Camp, of the University of California; and Mr. Alfred C. Shelton, formerly of the University of California.

The writer takes this occasion also to express his appreciation of the valued criticisms and suggestions furnished by Dr. Joseph Grinnell of the University of California under whose immediate supervision the work was carried on.



## C *ARBORIMUS*, A NEW SUBGENUS OF *PHENACOMYS*

### I GEOGRAPHIC DISTRIBUTION OF TYPE SPECIES AND SUBGENUS.

*Phenacomys longicaudus* True, the type species of the new subgenus, is found in southwestern Washington and northwestern California. *Phenacomys albipes*, tentatively referred to *Arborimus*, occurs in the same general locality. (See map, fig. 4, p. 137.)

### II ESSENTIAL CHARACTERS OF *Arborimus*.

Palate tending to be different posteriorly from that in the subgenus *Phenacomys*.

M<sup>3</sup> with second outer triangle tending to be closed off from posterior loop; posterior loop tending to be more rounded, and less emphatically drawn out antero-posteriorly than in *Phenacomys*.

Triangles and loops of M<sub>1</sub> tending to open into one another, except in *albipes*.

Antero-external loop of M<sub>2</sub> never closed off, tending to be smaller than in most examples of *Phenacomys*.

Outer triangle on M<sub>2</sub> tending to be smaller and to open into opposing triangles, except in *albipes*.

M<sub>3</sub> ordinarily simpler than in *Phenacomys*, practically three transverse crescents without external triangle.

Interorbital constriction tending to be narrower than in *Phenacomys*.

Tail proportionally decidedly longer than in *Phenacomys*.

Color a brilliant reddish, except in *albipes*.

Habit arboreal, except in *albipes*, nesting and apparently living entirely in trees.

Distribution, humid coast belt of southwestern Oregon and northwestern California, a section in which no specimen of the subgenus *Phenacomys* has ever been found.

### III DESCRIPTION OF *Phenacomys longicaudus* TRUE

#### 1 CRANIAL CHARACTERS

##### (1) Skull in general

Similar in general characters to that of *Phenacomys*. Crania of *Phenacomys (Arborimus) longicaudus* have broader brain-

case than those of *P. (Phenacomys) intermedius*, much as in *P. (Phenacomys) orophilus*. The narrower interorbital constriction is the most certainly diagnostic character of the crania of members of the new subgenus (see table of measure-

A Cranial measurements comparative of  
*Phenacomys (Arborimus) longicaudus* and *Phenacomys (Phenacomys) orophilus*

(All measurements in millimeters)

| Museum                 |         | Greatest length | Zygomatic width | Interorbital constriction <sup>1</sup> | Width of cranium outside external auditory meatus |
|------------------------|---------|-----------------|-----------------|--|---|
| No.                    | Sex     |                 |                 |  |   |
| Phenacomys orophilus   |         |                 |                 |  |   |
| 205916                 | ♂ ..... | 25.8            | 15.1            | 3.5                                    | 12.0  |
| 109103                 | ♂ ..... | 26.6            | .....           | 3.9                                    | 12.2  |
| 67327                  | ♂ ..... | 25.7            | 14.9            | 3.6                                    | 11.7  |
| 110249                 | ♀ ..... | 25.0            | 14.9            | 3.8                                    | 11.5  |
| Phenacomys longicaudus |         |                 |                 |  |   |
| 21145                  | ♂ ..... | 24.4            | 14.3            | 3.0                                    | 11.1  |
| 21148                  | ♂ ..... | 24.4            | 13.9            | 3.4                                    | 11.6  |
| 19983                  | ♀ ..... | 26.1            | 14.6            | 3.3                                    | 12.4  |
| 19174                  | ♀ ..... | 25.0            | 15.1            | 3.4                                    | 11.9  |
| 21149                  | ♀ ..... | 25.0            | 14.2            | 3.2                                    | 11.6  |
| 21143                  | ♀ ..... | 25.2            | 14.4            | 3.2                                    | 12.4  |
| 19973                  | ♀ ..... | 25.1            | 14.1            | 3.3                                    | 12.2  |
| 19130                  | ♀ ..... | 24.6            | 14.3            | 3.4                                    | 11.5  |
| 19984                  | ♀ ..... | 25.8            | 14.9            | 3.5                                    | 12.4  |

<sup>1</sup>Miller remarks (1897, p. 80) that the breadth of the interorbital region in *Phenacomys* is a character of trifling importance, which might easily disappear with increasing age. But the character as a good diagnostic feature would seem to hold between the series before me, since the specimens compared are good adults, with the examples of *orophilus* averaging older than those of *longicaudus*.

ments). Palate posteriorly tends to be different in *Arborimus*, usually having lateral pits a little deeper, sloping portion of median ridge longer, and lateral bridges more often present. In *Phenacomys* the lateral pits tend to be shallower, the sloping portion of the median ridge is shorter, in some specimens almost obsolete, and the lateral bridges are more often absent than present. There is overlapping between the subgenera in this respect. Young individuals of *longicaudus* tend to resemble *orophilus* and *intermedius*.

Enamel pattern in *Phenacomys longicaudus* simpler than in certain representatives of the subgenus *Phenacomys*, but not presenting any characters in all cases diagnostic of the new subgenus. The first and second upper molars are practically

identical with those in the subgenus *Phenacomys*, and will not be discussed separately. The front upper molar has, beginning anteriorly, a transverse loop, two inner triangles, one outer triangle, and a postero-external loop. The middle upper molar has transverse loop, one outer triangle, one inner triangle, and a postero-external loop.

(2) Back upper molar

Pattern practically as in the subgenus *Phenacomys*. Beginning anteriorly, the tooth shows a transverse loop, an external triangle, an internal triangle, a second outer triangle, and a postero-internal loop.

In the subgenus *Phenacomys* the outer portion of the posterior "trefoil" ordinarily opens into the inner portion, forming a figure crescentic or boomerang-shaped in outline, the concavity of the crescent or boomerang being directed forward. Sometimes the crescent or boomerang is symmetrical, but usually the inner arm is the heavier. In *Phenacomys longicaudus* the outer portion of the crescent tends to be closed off from the inner portion, forming a second triangle externally and a loop internally, the loop tending to be more rounded than is ordinarily the case in the subgenus *Phenacomys*.

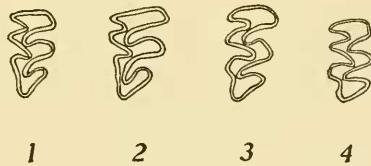


Fig. 1—ENAMEL PATTERN OF BACK UPPER MOLARS OF PHENACOMYS.

From left to right these belong to the following species: No. 1, *Phenacomys (Phenacomys) intermedius*; No. 2, *Phenacomys (Phenacomys) orophilus*; No. 3, *Phenacomys (Arborimus) albipes*; No. 4, *Phenacomys (Arborimus) longicaudus*. Traced from photograph. A little less than six times natural size.

Note the development of the second outer triangle and the general difference in outline posteriorly in the new subgenus *Arborimus*.

There is some variation in the tightness of the closure of the second outer triangle in *longicaudus*. In the young the triangle is scarcely formed. In its place is a channel, opening broadly both forward and back and showing on its external

outline a weakly developed salient angle which later becomes the strongly developed salient angle of the triangle. One specimen of *longicaudus* (No. 19976) is unusual in having the second outer triangle opening into the inner triangle forming with it a transverse loop which opens very narrowly into the posterior loop. In a few examples of *longicaudus* (Nos. 21143, 19130, 19174, 19985, and 21154) the second outer triangle opens narrowly into the posterior loop.

In all examples of the subgenus *Phenacomys* at hand, except in one specimen of *P. orophilus* (No. 101058), the outer portion of the crescent or boomerang is not closed to form a second outer triangle, but communicates, usually broadly, with the inner portion.

In the original description of the genus *Phenacomys*, Merriam states (1889, p. 31) that sometimes the outer loop of the trefoil is closed, giving the tooth two external closed triangles and a postero-internal loop. Elliot's illustration (1899b, p. 255) of the upper tooth-row of *olympicus* shows the second outer triangle closed as in *longicaudus*. A cut of the upper tooth-row of *orophilus* published by Merriam (1891, opp. p. 130, pl. III, fig. 3) shows a small second outer triangle closed off from the postero-internal loop, as in *longicaudus*. Similar relations hold in another illustration in the literature (Elliot, 1901, p. 167).

It is clear from these facts that *longicaudus* could not be certainly identified on the enamel pattern of the back upper molar. But there is an average difference between the situation in *longicaudus* and that in subgenus *Phenacomys*, in which latter, ordinarily, the crescent or boomerang looks as if it had been held in the middle while still soft and its arms pulled out anteriorly. In *Arborimus* the outer arm of the crescent becomes the second outer triangle, which is generally closed in both directions, and the postero-internal loop, which is rounded in outline and lies less in an antero-posterior position than the inner arm of the crescent in subgenus *Phenacomys*.

(3) Front lower molar

Agrees with all the species of the genus of which I have material before me in possessing an anterior tripartite trefoil,

with anterior, inner and outer loops all broadly communicating, three long inner and two short outer triangles, and a posterior transverse loop. Certain specimens (as *Phenacomys longicaudus* Nos. 19979 and 21150) have the outer loop of the anterior trefoil closed to form an additional outer triangle. In one specimen of *longicaudus* (No. 42621) both inner and outer loops of the anterior trefoil are constricted to form triangles, though neither triangle is completely closed. The small anterior loop in this specimen bends sharply inward. No. 42621, therefore, has a small anterior loop, four inner and three outer triangles, and posterior transverse loop.

The species of the genus differ more or less constantly in the tightness of closure of loops and triangles. There prevails in *longicaudus* the most open condition which I have observed in the genus; in *albipes* and *intermedius* the closure is tighter; and in *orophilus* it is tightest of all.

No. 21147 is unique among the specimens of *longicaudus* in having the inner reëntrant angles so deep that the second outer triangle is not in evidence. Ordinarily the second inner triangle is closed off from the second outer triangle, while the third inner triangle is not closed. In No. 19983, however, the reverse is true. In one or two examples the molar pattern is slightly different on right and left sides. Teeth which are much worn have the reëntrant angles transformed into lakes, and do not show the enamel pattern characteristic of earlier ages.

In most of the specimens of *longicaudus* the first inner triangle opens into the outer loop of the anterior trefoil, while in *albipes* and in a majority of the specimens of *orophilus* before me it is closed. In three specimens of *intermedius* a narrowly open condition is observed, but in the type specimen of *intermedius*, as figured by Merriam (1889, pl. IV, opp. p. 44), the triangle is closed. Two specimens of *longicaudus* (Nos. 21152, 21147) have the first inner triangle closed off from the outer loop of the anterior trefoil. In No. 19983 the triangle is open on one side but closed on the other, and it is only very narrowly open in two or three examples, notably No. 19130. In most young individuals of *orophilus* the first

inner triangle is not tightly closed, nor is it in *orophilus* No. 95080.

There are no characters in this tooth which distinguish the subgenus *Arborimus* from certain members of the subgenus *Phenacomys*. In Merriam's original description of the genus he uses the following language with reference to the front lower molar (1889, p. 31): "First lower molar with a posterior transverse loop, four greatly elongated internal triangles or digitations, of which at least two are completely closed, an anterior loop of variable shape, and three short external triangles, of which at least one is completely closed." In the illustration of the enamel pattern of *celatus* in Merriam's plate

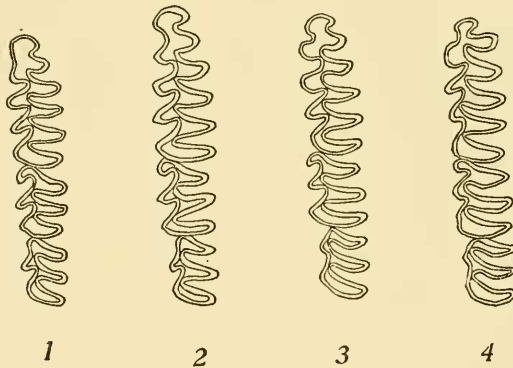


Fig. 2—ENAMEL PATTERN OF MANDIBULAR TEETH OF PHENACOMYS.

No. 1, *Phenacomys (Phenacomys) intermedius*; No. 2, *Phenacomys (Phenacomys) orophilus*; No. 3, *Phenacomys (Arborimus) albipes*; No. 4, *Phenacomys (Arborimus) longicaudus*. Traced from photograph. About six and one-fourth times natural size.

Note that in *Arborimus* the antero-external loop of  $M_2$  is not closed and tends to be smaller than in *Phenacomys*; note the peculiar arrangement of the second outer triangle in *longicaudus*; and finally note the comparative simplicity of  $M_3$  in *Arborimus*.

IV, opposite page 44, the first inner triangle is shown opening broadly into the outer loop of the anterior trefoil as in *longicaudus*. In this specimen also the first inner triangle is shown to open broadly into the first outer triangle. On plate III, facing page 42, the first inner triangle in *P. ungava* is shown opening narrowly into the first outer triangle. Miller (1896, p. 41) has figured the enamel pattern of *celatus*. According to his illustration the first inner triangle opens narrowly both forward and back. These are the only instances I have noted in the literature in which conditions are found similar to those in *longicaudus*.

It seems safe to conclude that *longicaudus* is characterized, with qualifications as above noted, by a more open condition of the loops and triangles of this tooth than in the subgenus *Phenacomys*.

(4) Second lower molar

Similar in pattern to *Phenacomys intermedius*, the type of the genus *Phenacomys*. Small antero-external loop, elongated antero-internal triangular digitation, one short outer triangle, one long inner triangle, and a posterior transverse loop.

The small antero-external loop is never closed in *longicaudus*. In one specimen of *intermedius* (No. 174425) the loop is larger than in any specimen of *longicaudus*, with the possible exception of No. 21143, opening broadly into the opposing triangle; in another specimen of *intermedius* (No. 174431) the antero-external loop is only narrowly open; while in a third (No. 174432) the loop is large and opens broadly. All specimens of *orophilus* at hand, with the exception of Nos. 205916 and 67327, have this loop tightly closed off from the opposing triangle. In Merriam's figure 7, illustrative of the genus *Phenacomys* (1889, p. 31) the loop is tightly closed. In his plate III, facing page 42, the antero-external loop both in *celatus* and *ungava* is broadly open as in *longicaudus*. Plate IV, opposite page 44, shows the antero-external loop opening broadly in *latimanus* as well as in *celatus* and narrowly in *intermedius*. In Miller's figure of *celatus* (1896, p. 41) the same relations are shown.

The outer triangle in *longicaudus* tends to be of comparatively small size and not tightly closed off from the antero-internal triangle and the opposed inner triangle. In most specimens the outer triangle opens rather broadly into the opposed inner triangle and narrowly, if at all, into the antero-internal triangle. In *intermedius* the outer triangle is larger than in *longicaudus*, and is closed off in both directions. In *orophilus* there is a considerable range of individual variation in this respect. In four adult examples (Nos. 109103, 67327, 110249, and 205916) the outer triangle is large and is closed.

According to Merriam's plate IV (1889, opp. p. 44) the outer triangle in *latimanus* opens very narrowly anteriorly.

Summarizing, it may be said that while in the subgenus *Phenacomys* the antero-external loop is often closed, it never is in *Phenacomys (Arborimus) longicaudus*; there is also apparent a tendency in the latter for the outer triangle to be smaller and more open than in the subgenus *Phenacomys*.

(5) Third lower molar

Typical of the genus, being made up of three transverse triangular digitations connected along the outer border of the tooth. Tending to be simpler in *P. longicaudus* than in the subgenus *Phenacomys*, in which there is often if not usually a small outer triangle pinched off opposite the middle transverse triangular digitation.

In one specimen of *longicaudus* (No. 21150) this little outer triangle is definitely outlined, though it is not closed off. Similar conditions obtain in several other specimens. There is considerable variation in *orophilus*. In two specimens (Nos. 31249 and 75029) no triangle is outlined, and this is true in several young examples also; but in most adult examples the little triangle is emphasized and tightly closed. In *intermedius*, type of the genus, the triangle is well developed, being practically closed in Nos. 174431 and 174432, but opening posteriorly in the right molar of No. 174425.

Summarizing, in *longicaudus* an outer triangle on the third lower molar is never isolated in the sense of being tightly closed. In the subgenus *Phenacomys* there is a tendency for an outer triangle to be isolated in this manner.



## 2 EXTERNAL CHARACTERS

## (1) General coloration

While certain young examples (notably Nos. 137, 138, 139, Univ. Oreg. Mus.) are somewhat paler than the rest, the entire series of thirty-three skins before me is remarkably uniform in general coloration, being cinnamon dorsally, paling to light ochraceous-buff on the sides, and becoming white ventrally. Tail usually colored a very dark brown, near seal brown, with no demarcation between dorsal and ventral coloration.

## (2) Dorsal coloration

A rich cinnamon, the exact hue varying from near orange-cinnamon (as in No. 21149, a specimen of middle age) to near ochraceous-buff (as in No. 19980, a very young specimen). The majority of the specimens are cinnamon or pinkish cinnamon on the back, and all have a greater or less insprinkling of spiny black hairs, which tend to give a darker appearance than would otherwise be the case. Eight young examples are quite close to No. 19980 in coloration.

The hairs of the contour pelage are deep plumbeous basally, the lighter portion of the shaft being confined to the tip. On nose and around eyes the hairs are shorter and lack the plumbeous bases. In most of the specimens the short hairs on the extreme tip of the nose are near light seal brown. Whiskers silvery or blackish brown, the silvery hairs often having blackish-brown bases. The combination of short ears and rather long hair makes the ears inconspicuous. In some specimens (notably Nos. 19985, 21145, 19984, 19975, 19980, 19978) the ears are almost concealed. In all examples the long hairs of the body pelage overlie the opening into the ear. The pinna of the ear itself is very thinly haired, within and without, with hairs similar in coloration to those making up the contour pelage of the body, except that there is a tendency for the plumbeous bases to be absent. Toward the base of the pinna the typical body pelage is encountered.

Forefeet dorsally with a shade of the buff or cinnamon series somewhat paler than that of the dorsal coloration, ordinarily white on the fingers, but sometimes washed with very pale buff; ventrally white; palm naked; hairs about bases of claws exceeding claws in length. Hind feet whitish, washed with

buffy on toes dorsally, as in No. 19174; or having black hairs insprinkled and a darker shade of buffy, as in Nos. 19974 and 19983; hairs about bases of claws often exceeding claws in length. Sides of body paler than back; the spiny black hairs fewer in number. In a typical example (No. 19174) the color grades from near orange-cinnamon dorsally to light ochraceous-buff laterally.

The peculiarities in coloration of a specimen collected at Meadows, Lane County, Oregon, have already been commented on in the literature (Miller, 1897a, p. 85; Merriam, 1901, p. 126; and see below, p. 131).

### (3) Ventral coloration

White, sometimes with plumbeous bases of hairs showing through to some extent, often with the faintest possible wash of buffy. In adult females the positions of the two pairs of abdominal mammæ are marked by sparsely-haired circular patches a quarter to one-half inch in diameter. Hairs of throat and of nipple patches have no plumbeous bases. Sometimes hairs posteriorly on belly in vicinity of nipple patches also lack plumbeous bases.

Tail varying in coloration, in different examples, from pinkish-cinnamon to blackish-brown. Although there is in some specimens the faintest possible tendency toward ventral paling, in a large majority there is no discernible difference in coloration between the upper and lower sides. Most of the series have the tail tipped with a pencil of blackish-brown hairs. In No. 21153 all the tail except the tip is pinkish-cinnamon. Consequently the blackish-brown tip is very conspicuous. Ordinarily the general tail coloration is so dark that no contrast is observable.

### (4) Length of tail

Miller (1897a, p. 79), in his key to the genus *Phenacomys*, sets off *longicaudus* as having a tail forty per cent of its total length, while the remaining species, including *ungava*, *latimanus*, *intermedius*, *preblei*, and *orophilus*, are grouped as having tails only twenty-five per cent of total length.

An examination of the available series of thirty-seven specimens of *longicaudus*, in connection with the study of the other examples of *Phenacomys* at hand and of all published measurements, enables the writer to confirm the validity of this

grouping. Of the series of *longicaudus*, No. 19985, a young adult, has the tail 44.2 per cent of its total length. No. 19976, also a young adult, is next, with the tail 42.5 per cent of total length. The largest and oldest individual of all, No. 19984, follows with tail 42.4 per cent total length. The smallest and youngest example of *longicaudus* measured to date (No. 20657, preserved in alcohol) has tail only 25.7 per cent of total length. Young animals are all characterized by low ratios, and as the scale of age is ascended the ratio increases.

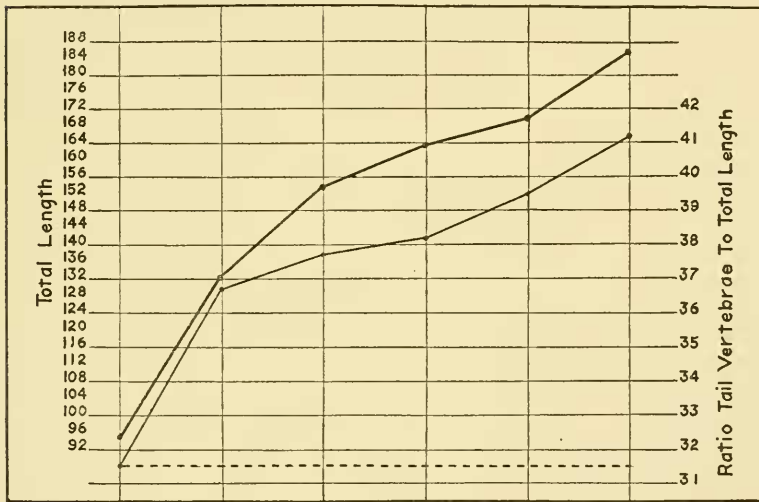


Fig. 3—INCREASE IN RATIO OF LENGTH OF TAIL VERTEBRÆ TO TOTAL LENGTH WITH AGE.

The heavy black line represents the actual total length (correlated with age); the light black line the ratio of the length of the tail vertebrae to total length. Each round dot represents the average for six individuals. The pair of dots on each vertical line pertain to the same six individuals. Read scale for actual total length on the left side of the diagram, and scale for ratio of the length of the tail vertebrae to total length on the right side. Note that if the ratio of the length of the tail vertebrae to total length remained constant with increasing age at the figure for the smallest group, the ratio would be indicated by a horizontal line, as dotted in the figure. But instead of this, the ratio undergoes a steady increase with age.

Of the other species of the genus, *P. albipes* makes the nearest approach to *P. longicaudus*, the two known specimens of this form having ratios of tail vertebrae to total length of 36.9 and 40.0 per cent respectively. Three skins of *P. inter-*

*medius* at hand (Nos. 174431, 174425, and 174432, U. S. Nat. Mus.) show ratios of 28.6, 34.3, and 29.3 per cent respectively; while two skins of *orophilus* (Nos. 109103 and 109102, Biol. Surv. Coll.) show ratios of 30.5 and 28.1 respectively. Of thirty-six specimens, representing eleven different species of the subgenus *Phenacomys*, the measurements of which are recorded in the literature, in only two does the ratio exceed 26.0 per cent, and in the majority it falls below 25.0. More

B External measurements of three species of the genus *Phenacomys*  
(All measurements in millimeters)

| Museum No. | Sex       | SPECIES AND LOCALITY                                    | Total length | Tail vertebrae | Hind foot | Ratio tail vertebrae to total length |
|------------|-----------|---|--------------|----------------|-----------|--------------------------------------|
|            |           | <i>Phenacomys albipes</i>                               |              |                |           |                                      |
| 97236      | ♂ ad.     | California: Humboldt Bay (Arcata<br>—in redwoods) ..... | 168          | 62             | 19        | 36.9                                 |
| 797        | ♂ ad.     | Vida, Lane Co., Oregon.....                             | 165          | 66             | 19        | 40.0                                 |
|            |           | <i>Phenacomys orophilus</i>                             |              |                |           |                                      |
| 109103     | ♂ ad.     | California: Tuolumne Meadows....                        | 154          | 47             | 18        | 30.5                                 |
| 67327      | ♂ old ad. | Montana: Bear Tooth Mountains..                         | 142          | 33             | 17        | 23.2                                 |
| 110249     | ♀ yg. ad. | California: Mt. Lyell .....                             | 153          | 41             | 17        | 26.8                                 |
| 110251     | ♂ yg. ad. | California: Mt. Lyell .....                             | 121          | 28             | 17        | 23.1                                 |
| 23849      | ♂ yg.     | Idaho: Salmon River Mountains..                         | 120          | 28             | 18        | 23.3                                 |
| 109102     | ♀ yg.     | California: Tuolumne Meadows....                        | 114          | 32             | 16        | 28.1                                 |
|            |           | <i>Phenacomys intermedius</i>                           |              |                |           |                                      |
| 174431     | ♂ ad.     | Alberta: Head of Smoky River....                        | 98           | 28             | 19        | 28.6                                 |
| 174425     | ♀ ad.     | British Columbia: Moose River....                       | 105          | 36             | 19        | 34.3                                 |
| 174432     | ♀ ad.     | Alberta: Head of Smoky River....                        | 106          | 31             | 19        | 29.3                                 |

than that, the average ratio of thirty-one additional specimens, representative of the subgenus *Phenacomys*, falls below 26.0 per cent. These specimens constitute all of which measurements have been found by the writer in the literature.

Miller (1896, p. 24) asserts that length of tail in the *Microtinae*, being more unstable than certain other characters because more readily modified to fit a species to special requirements of its environment, is less important than these other characters in the diagnosis of subgenera. It would seem to the writer, however, that such a marked difference as seems to hold in this respect between the *albipes-longicaudus* group on the one side and the other species of *Phenacomys* on the other should be regarded as of at least subgeneric value.

## (5) Tuberculation of feet and the number of mammæ

A young example of *Phenacomys longicaudus* (No. 20658), preserved in alcohol, has five tubercles on the fore feet; the reduction of the thumb to a small tubercle makes the fore feet appear to have an additional tubercle. The hind feet are six-tuberculate.

*Longicaudus* has two pairs of mammæ placed far back on the belly. The only reference to the number of mammæ in the genus *Phenacomys* which I have been able to find in the literature is that of Miller (1897b, p. 22), in which a female of *P. latimanus* is stated to have eight mammæ, four pectoral and four inguinal. A difference in number of mammæ may characterize the two subgenera.

(6) The type of *Phenacomys longicaudus* True

This specimen has been several times described and the condition of its skull commented on (True, 1890, p. 303; Miller, 1897a, p. 85; Merriam, 1901, p. 126; Lyon and Osgood, 1909, p. 96). Tooth pattern in No. 19974 of our series from Mendocino City practically the same as in the type; and external characters show clearly that specimens in our collection are almost identical with the type.

## (7) The specimen from Meadows, Lane County, Oregon

Miller (1897a, p. 85) has described the aberrant specimen from Meadows, Lane County, Oregon (♀, No.  $\frac{30649}{42621}$  U. S. Nat. Mus., Biol. Surv. Coll., taken April 13, 1891), in the following words: "Head, back and sides pale yellowish drab, the fur light bluish plumbeous at base and sprinkled with inconspicuous dark hairs; belly grayish white, the bluish bases of the hairs showing through irregularly; tail indistinctly bicolor, light slaty gray above and at tip, whitish mixed with gray below; feet silvery white." Merriam (1901, p. 126) refers to the same specimen as being pale buffy fulvous, and remarks that it seems to be a partial albino.

## (8) Pelages

Specimens are available representative of every month in the year except September and December. Examples with the longest hair were collected during the winter months (notably No. 19130, taken January 6, and No. 19174, March 27).

The shorter the pelage the greater is the tendency for the plumbeous bases of the hairs ventrally to show through, consequently differences in length of pelage are more readily perceptible below than they are above. Applying this test to our series of *P. longicaudus* it is noted that spring and summer skins tend to have shorter pelage than those taken at other times of year.

No. 21143, collected April 20, has the pelage comparatively thin. Ten specimens, taken October 24 and 25, are not conspicuously different from those collected in July.

There is a not readily tangible tendency toward paleness in the summer skins. The slightly darker shade noted in the winter examples is apparently due to the longer cinnamon tipping rather than to any real difference in hue.

No molt lines or other indications of molt, aside from the slight difference in length of hair, are observable. Whether there is a definite time of molt cannot be stated. It is not improbable that there is a gradual hair renewal late in the fall, perhaps during November, and that the "summer pelage" is simply the worn winter pelage remaining over from this molt.

#### IV RELATIONS OF *Phenacomys albipes* TO THE TWO SUB- GENERA OF *Phenacomys*

The complex of its characters relates *Phenacomys albipes* more closely to *P. longicaudus* than to any other known form of the genus, as was implied by Merriam in the original description (1901, p. 125). For thirteen years the type specimen of *albipes* remained unique, and it is only recently that a second specimen has been collected (see Jewett, 1915, pp. 37-38).

Cranially *Phenacomys albipes* stands off by itself. Its skull, as compared with that of *orophilus*, *intermedius*, and *longicaudus*, has an appearance of length and narrowness (see Plate 15). Testing by actual measurement we find that there is no clear dimensional difference in greatest length (see tables of cranial measurements), *albipes* being exceeded by four of the nine specimens of *longicaudus* measured, and by three of the four specimens of *orophilus* measured. The zygomatic arches, however, do not spread so widely in *albipes* as in *longicaudus*, *orophilus* or *intermedius*. In fact, this dimen-

sion, as given in the tables of measurements, is less in *albipes* than in any specimen of these species measured, with one exception, an example of *intermedius* (No. 174431), in which the dimension is the same as that in *albipes*. In width of

C Cranial measurements comparative of  
*Phenacomys (Arborimus) albipes* and *Phenacomys (Phenacomys) intermedius*

(All measurements in millimeters)

| Museum No.                    | Sex | Species | Greatest length | Zygomatic width | Interorbital constriction | Width of cranium outside external auditory meatus |
|-------------------------------|-----|---------|-----------------|-----------------|---------------------------|---|
| <i>Phenacomys albipes</i>     |     |         |                 |                 |                           |   |
| 97236                         | ♂   | .....   | 25.6            | 13.8            | 3.3                       | 11.3  |
| 797                           | ♂   | .....   | 25.1            | .....           | 3.7                       | 11.2  |
| <i>Phenacomys intermedius</i> |     |         |                 |                 |                           |   |
| 174431                        | ♂   | .....   | 23.8            | 13.8            | 3.7                       | 11.0  |
| 174425                        | ♀   | .....   | 24.9            | 14.2            | 3.6                       | 11.0  |
| 174432                        | ♀   | .....   | 24.3            | 14.3            | 3.7                       | 11.1  |

interorbital constriction one specimen of *albipes*, No. 97236, agrees with *longicaudus*, while the other, No. 797, is closer to *intermedius* and *orophilus*; in width of cranium outside of external auditory meatus the examples of *albipes* are less than those of *orophilus* but greater than those of *intermedius*. Eight of the nine comparable specimens of *longicaudus* exceed *albipes* in this measurement.

Back upper molar in *albipes* has the outer portion of the posterior crescent closed off to form a second outer triangle. In the type (No. 97236), the second outer triangle is closed off from the inner portion of the crescent in this tooth on both sides. In the second specimen (No. 797), there is a tendency for the second outer triangle on the left hand side to open very narrowly into the interior part of the crescent. In this character *albipes* is closest to *longicaudus*. The inner loop is intermediate in position and outline between *orophilus* and *longicaudus*, tending, in No. 97236, in the direction of *orophilus*, and in No. 797 in the direction of *longicaudus*. Whereas in the type (No. 97236) the triangles and loops of the front lower molar are for the most part closed off from one another, in No. 797 they tend narrowly to intercommunicate. The tight closure of these loops and triangles is observed often in, if not characteristic of, the subgenus *Phenacomys*.

whereas the open condition is typical of *longicaudus*. Antero-external loop of second lower molar as in *longicaudus*. Outer triangle on same tooth moderate in size, often opening very narrowly forward or back, practically intermediate in condition between *longicaudus* and the *orophilus-intermedius* series. Back lower molar as in *longicaudus*.

In coloration dorsally and laterally *albipes* has been described as "grizzled bister" differing from the grayish or light brownish *orophilus-intermedius* series in being darker, and from *longicaudus* in being browner. Its general aspect is much like that of *Evotomys californicus*. The coloration of the lighter hairs is of a tint a little paler than the cinnamon of *P. longicaudus*, from which *albipes* differs markedly in having a much larger proportion of black hairs. Laterally there is an inconspicuous paling, the result of a slight increase in the number of hairs of a cinnamon or buffy hue. Ventrally *albipes* is white, as in *longicaudus*, but with a faint wash of buffy, as in *Evotomys californicus*. Feet white. Tail sharply bicolor, "dusky" above and "broadly whitish" below. The tail is also longer than in any other species of the genus except *longicaudus* (see p. 129, above).

As may be inferred from the fact that only two specimens of *albipes* have been taken to date the habits of the form are practically unknown. Dr. Walter K. Fisher, who collected the type specimen, informs the writer that the type was taken in a trap set close to the base of a redwood perhaps two feet in diameter, which formed one of a clump. The trap was set on top of a small rotten log, which leaned against the tree and was covered with "needles." The clump was made up of second growth redwoods and the general surroundings were dry. The second specimen (Jewett, 1915, p. 38), was collected among rocks at the side of a small stream where it flows through a dense forest of spruce and fir timber. At this point both banks of the stream were lined with an almost impenetrable jungle of salmon-berry bushes and sword fern, where jumping mice and deer mice, as well as several species of shrews, were collected. Thus there is no evidence of any arboreal habit in *Phenacomys albipes*.

Summarizing, it should be noted that *Phenacomys albipes* resembles *P. longicaudus* in that there is present on the back



upper molar a second outer triangle, which is practically closed off from the inner loop, the antero-external loop on the second lower molar is open, the enamel pattern of the third lower molar is nearly identical, the geographic range is similar, and the proportionate length of the tail is nearly the same. It differs from *longicaudus* in being darker, in having a faint wash of buffy on the white ventral surface of the body, in its bicolored tail, in the general length and narrowness of its skull, and in its, so far as known, exclusively terrestrial habit. It is practically intermediate between the *orophilus-intermedius* series on the one hand and *longicaudus* on the other in width of interorbital constriction, outline and position of postero-inner loop on back upper molar (closer to *longicaudus* than to the *orophilus-intermedius* series in this character), and outline of outer triangle on second lower molar (perhaps closer to the *orophilus-intermedius* series in this character).

There are several alternatives open in the matter of the disposition of *Phenacomys albipes*. It may be left "of uncertain status"; it may be accorded separate subgeneric rank; or it may be referred to one or the other of the subgenera *Phenacomys* and *Arborimus*. In view of the small amount of material available, there is much to be said in favor of leaving it for the present "of uncertain status." The peculiar slender appearance of its cranium might be regarded as of separate subgeneric value, if it were more striking, or if there were associated with it other characters of importance. Since most of the available evidence seems to point to the disposition of *albipes* as a member of the subgenus *Arborimus*, the species has been assigned thereto by the present writer, but in the absence of more material and information it is emphasized that such reference must necessarily be no more than tentative.

## D DISTRIBUTION AND HABITS OF *PHENACOMYS LONGICAUDUS* TRUE

### I DISTRIBUTION

#### 1 IN TIME

No fossil material whatever referable to the genus is known. "*Arvicola intermedius* Newton (see Miller, 1896, pp. 75, 76) from the late Pliocene Forest Bed of Norfolk, England, referred to *Phenacomys* by Nehring, has recently been associated with a number of other fossil forms in the genus *Mimomys* Forsyth Major. As stated by Hinton with reference to the genus *Mimomys* (1914, p. 474), "its members are amongst the earliest microtines in Britain, having been detected in the late Pliocene Norwich Crag." Consequently this genus is of great interest, although its generalized enamel pattern with reëntrant angles approximately equal shows that it cannot be closely related to *Phenacomys*.

#### 2 IN SPACE

Specimens have been actually taken as follows: In Oregon: Marshfield, Coos County; Meadows, Lane County; Eugene, Lane County. In California: Chaparral Mountain, above Maplecreek Post Office, near "Big Bend," Mad River, Humboldt County; Cuddeback, Humboldt County; Carlotta, Humboldt County; Mendocino City, Mendocino County; Lierly's Ranch, four miles south of Mt. Sanhedrin, Mendocino County.

There is little doubt that the tree mouse occurs at many other localities in this general region. Mr. Aurelius Todd,

Fig. 4—KNOWN RANGE OF *PHENACOMYS LONGICAUDUS*, WITH RECORD STATIONS OF ALL THE *PHENACOMYS* KNOWN TO HAVE BEEN TAKEN IN CALIFORNIA AND OREGON.

(See map on opposite page.)

- Localities where *Phenacomys orophilus* has been collected
- ▲ Localities where *Phenacomys albipes* has been taken.
- Localities where *Phenacomys longicaudus* has been collected.
- ⊗ Localities where *Phenacomys longicaudus* is known to occur, but no specimens collected as yet.
- ▣ Area within which *Phenacomys longicaudus* is known to occur.

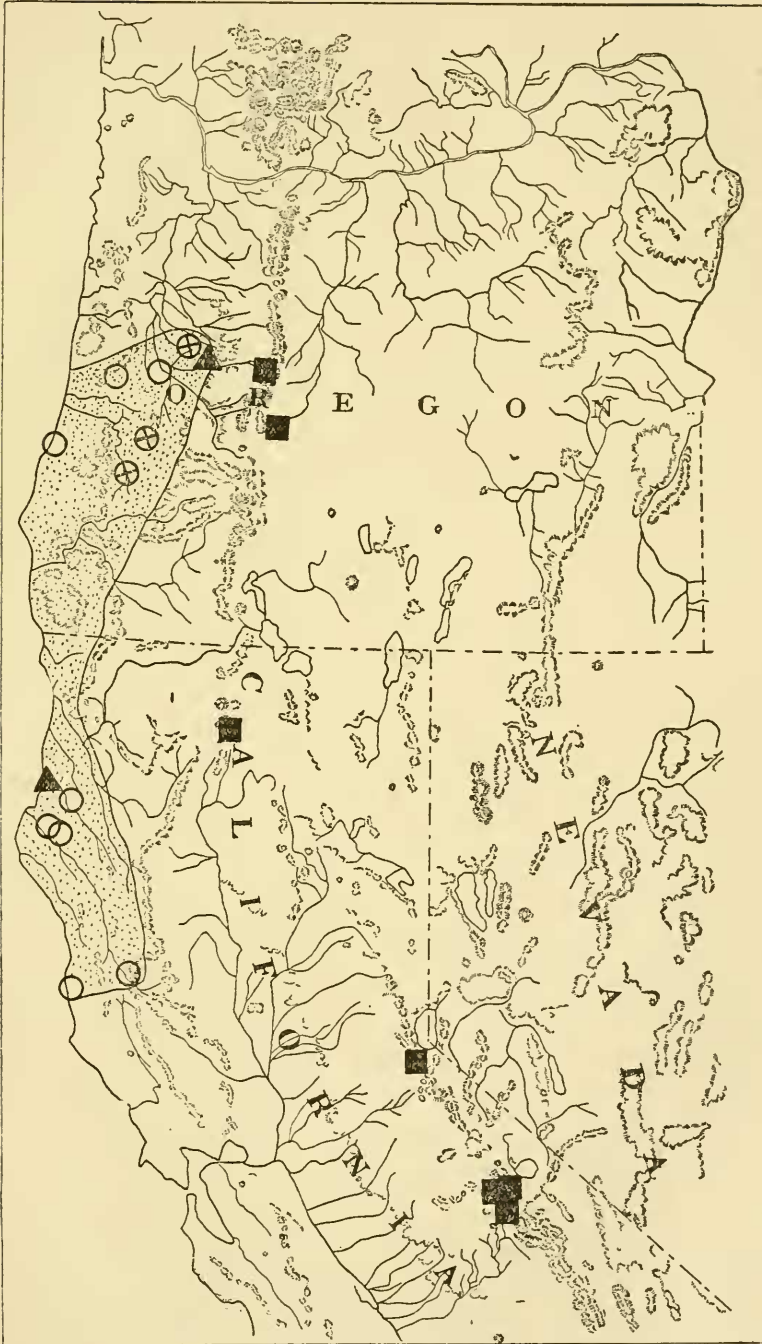


FIG. 4 (See caption on opposite page.)

to whom credit belongs for first calling the attention of scientists to the species, asserts (1891, p. 241) concerning its occurrence: "My first discovery of this animal was in June, 1886, in the valley of Elk Head, on the headwaters of Elk Creek, a tributary of the South Umpqua River, and some seven miles east of Voncalla, Douglas County [Oregon], while out looking for birds' nests . . . I have . . . found their nests down Elk Creek, along the Coquelle River, in Coos County, in southern Douglas County, and also on the upper Willamette tributaries, in Lane County, and believe it will yet be found in Washington and perhaps through the whole of the northern coast." Maps of Oregon, which the writer has examined, show two Elk Creeks tributary to the Umpqua River. Elk Head is located on the Elk Creek tributary to the main river, not tributary to the South Fork of the Umpqua. Voncalla is spelled Yoncalla on recent maps (1908, 1910), and Coquelle is rendered Coquille on the same maps.

In the original description of *Phenacomys longicaudus* (True, 1891, pp. 303-304) there is quoted a letter from Todd in which is contained the only reference I have seen to the occurrence of the tree mouse in Curry County.

Mr. Alfred C. Shelton, field naturalist of the University of Oregon, tells me that he has located colonies in the vicinity of Mabel, Lane County, and Melrose, Douglas County; while Mr. C. I. Clay, of Eureka, California, writes that on June 16, 1915, he observed a number of *Phenacomys* nests along the road between Ferndale and Capetown, on the ridge just north of Cape Mendocino and very close to the coast.

Upon this showing it is not unlikely that the species is far more abundant and widespread than the examples now contained in museums would indicate.

## II HABITS

### 1. GENERAL HABITAT

Characteristically, perhaps exclusively, arboreal. That the tree mouse ever comes to the ground of itself for the purpose of subserving its own specific economy remains to be demonstrated. In Todd's letter of transmittal which ac-

accompanied the shipment of the first specimen it is asserted that so far as could be found out, *Phenacomys longicaudus* lives exclusively among the boughs and branches of *Abies douglassi* (= *Pseudotsuga taxifolia*). Farther on Todd modifies this statement by remarking that tracks, which he thought were made by these little animals, had been seen in the snow around the trees. "They could be tracked," says Todd, "up and down the tree, but to no great distance from it, and were most likely in search of food." In a contribution to the West American Scientist (1891, p. 242) Todd again calls attention to the tracks he has seen around the trees, but specifically disclaims positive knowledge that they were made by *Phenacomys*.

Wilder gives it as his opinion that they must occasionally come to the ground, though it is to be doubted whether they spend much time there.

Clay says that in order to reach the tree containing the family nest, the males in some instances would have to descend to the ground. This is on the theory (see p. 153) that males live for at least a part of the time in small nests separate from those of the females.

All the clear evidence at hand shows that tree mice are dependent on the trees in which they live for food, home and drink. I have not seen nor can I find any record of any object found in any nest of *Phenacomys* indicating that it visits the ground. All nests at Mendocino City were found in grand firs (*Abies grandis*). The only piece of nest material not derived from this tree was a twiglet of Bishop pine (*Pinus muricata*), which was probably brought in by way of the tree branch route.

## 2 KINDS OF TREES INHABITED

Nests of *Phenacomys longicaudus* have been found in three conifers, *Picea sitchensis*, *Abies grandis* and *Pseudotsuga taxifolia*. Our field party in 1913 found nests in both the latter-named species, those at Mendocino City being in grand firs, while those at Lierly's and elsewhere were in Douglas firs.

So far as Todd was aware (1891, p. 240) the tree mouse was found only in the branches of the Douglas fir. In fact, all published records of nests which I have seen refer to their

occurrence in this tree alone. Clay reports that although the Douglas fir seems to be preferred, he has found many nests in the lowland (or grand) fir in the Mad River country (Humboldt County, California), and has taken several from the Sitka spruce. His record of nests in the Sitka spruce are so far unique.

It is quite probable that the larger numbers and general availability of the Douglas fir in the area of occurrence of the tree mouse have much to do with the observed occurrence of most of the nests in trees of that species.

### 3 COLONIAL TENDENCY

Although Wilder says that he has never found the *Phenacomys* in Humboldt County nesting in colonies, the experience of other investigators in other places shows that there is a pronounced grouping tendency observable. At Mendocino City, for example, our party made studies of two groups or colonies of nests, and all nests observed later exhibited a similar colonial arrangement. It should, however, be stated that in no case were the nests *closely* grouped, though they were located in the same general section of forest. Clay asserts that they live in colonies as a rule, although they spread to isolated positions in individual cases, and cover a vast expanse of territory.

One colony studied at Mendocino City was located on a flat north of town, in a grove of tall *Abies grandis* intermixed with scattering Bishop pines. The second was found on the side of a ravine a little farther to the north. Here, although the grand firs formed an almost pure stand, there were a few Douglas firs and an occasional Bishop pine. Examples of *Phenacomys* were taken in both these colonies.

Another colony was later located in large Douglas firs in an isolated position on the south-facing slope of a small hill, near the Eden Valley road, four miles north of Hearst, Mendocino County, California. A group of nests resembling those of gray squirrels, and possibly now belonging to *Phenacomys longicaudus*, was also encountered in a grove of Douglas firs about 500 feet above the South Fork of Eel River, and a mile distant therefrom, on the north side, four miles east of Hearst. Shortness of time did not permit of its examination.

Still another colony was found in the Douglas firs immediately south of Lierly's Ranch, four miles south of Mount Sanhedrin, Mendocino County, California. One tree mouse was here secured.

At Mendocino City thirteen nests were carefully examined. In eight of these animals were actually found. In the first colony there were about a dozen nests; in that on the side of the ravine, seven or eight. The colony north of Hearst contained about the same number, while at Lierly's there were more, although some of the nests observed in that locality may have belonged exclusively to *Sciurus griseus*.

#### 4 OBSERVED MOVEMENTS

*Phenacomys longicaudus* does not seem to possess any extraordinary agility, quickness, or aggressiveness of movement. Wilder says the mice are quick to leave the nest when the latter is disturbed, and remarks that while sometimes they are caught in the nest they are more easily caught on the ground, where, although not really slow, they are a little clumsy. Shelton relates an instance where a tree mouse left the nest just as the observer came on a level with the structure. It ran out to the tip of a branch and was there secured by means of a shot pistol. The same observer records an instance of the frightening of a *Phenacomys* from its nest, the animal showing remarkable agility, going from tip to tip of the fir boughs with speed and ease, and so running from tree to tree until finally it escaped into the branches of an old cedar (*Thuja plicata*), the fourth tree from the nesting site. This record of remarkable agility was not borne out by our observations, according to which the animals ran rather slowly and uncertainly along the twigs on which we saw them, and seemed on the whole rather slow-moving. Several were caught with the bare hands in the trees. One tree mouse, which reached the ground, exhibited more speed there than any we saw in the trees. It is quite possible, though on this point there is no evidence, that *Phenacomys longicaudus* is strictly nocturnal and is bewildered by the light of day.

The unwillingness of the tree mice to leave the nest was quite evident. Ordinarily the occupants would remain until much of the structure had been dissected away. In one

instance an adult female and a half-grown young individual were taken from the *last double handful* of the nest-mass remaining in the tree.

The tree mice when caught did not ordinarily defend themselves with energy, although one young individual seized a finger of its captor and bit hard enough to draw blood.

#### 5 VOICE

Wilder asserts that when individuals of *Phenacomys longicaudus* are caught they utter a mouse-like squeak. Only one of those taken by us was heard to utter a sound. This was a juvenile individual which, upon being seized, squeaked plaintively.

#### 6 FOOD AND DRINK

At Mendocino City we always found green twigs on and in occupied nests. The leaf of a grand fir was found in the mouth of one individual, and the stomachs and intestines of all those examined were brilliant green. Microscopic examination of cross-sections of the fir needles discloses the fact that all the fleshy substance of the needle including the vascular bundles is eaten away by the tree mouse, the only portions left being the two resin ducts which traverse the entire length of each needle. These filamentous resin ducts have quite naturally been mistaken for midribs by some observers. The outer or cortical portions of young shoots are also used as food, in this case resin ducts and all being eaten. It is probable that the chief food of the species is derived from the needles and young shoots.

In a colony on Chaparral Mountain, on the slope above Maplecreek Postoffice, Humboldt County, California, which was studied by Clay, the top of practically every inhabited tree was dead. Many nests were found by locating the dead-topped trees. "The nest was sure to be there," says Clay, "and was always inhabited." In some cases in which the nest was low in the crown of the tree and far out on a limb, the bark would not be touched, but in the dead-topped trees small runway-like trails were noticed over the trunk where the bark had been stripped away. Sometimes these trails ran together making a wide exposed place. The tree was cut



always at the exact level of the nest, or the point of junction of the nest-limb with the tree. "Many trees were bushed out at the top as though they had been cut, rotted off . . . and then taken sprout; some bushing out, some forking, and some growing up in a deformed top." Examination of these disclosed furrow-like ridges in the bark, where Clay concludes the trees had been cut many years ago. Tooth marks were plainly visible in some of the more recently stripped places, so that Clay is certain the cutting is done by *Phenacomys*, though he does not know whether the bark is eaten or not.

Because of the dead tree-tops, the semi-isolated nature of the grove in which it was located, and the age of the nests, it was concluded that this colony was a very old one. It is implied, furthermore, though Clay does not permit himself to make a positive statement in this regard, that only the trees containing old nests or which had been inhabited for a long time showed the phenomena of the dead tops. The absence of dead-topped trees in the vicinity of Carlotta where nests were studied by Wilder is explained on the supposition that *Phenacomys* occupation in that neighborhood has been of comparatively short duration; and the additional suggestions are tentatively propounded, that large trees are not subject to the attacks to which the smaller ones are liable; that possibly the tree mice feed on bark only intermittently; or that it may be that the bark of older trees is not palatable. It seems that the Chaparral Mountain colony was located in small firs, while occupied trees at Carlotta are of larger size.

Although it must be admitted that the circumstantial evidence submitted by Mr. Clay is strong, still it ought to be remembered that bark damage and tree destruction by *Phenacomys longicaudus* is unconfirmed to date by any other observer, and it is possible, if not probable, that phenomena due to some other local cause or condition on Chaparral Mountain have been erroneously associated with the tree mouse.

One animal kept by Mr. Clay in captivity would not eat grain, grass, or meal, finally dying apparently for lack of proper feeding.

The area of occurrence of the tree mouse falls for the most part within the humid coast province or faunal area, a region characterized by frequent fogs, high relative humidity of the

air, and moderately heavy rainfall. It is quite probable that the animal's need of moisture is supplied by the water which gathers on the foliage of the trees in which it lives, if, indeed, it needs more moisture than is contained in its food.

#### 7 HOME RANGE OF THE INDIVIDUAL

The fir trees in which our party found colonies of *Phenacomys longicaudus* were close together, and transit from tree to tree by way of the foliage route would be comparatively easy. In one nest a branchlet of Bishop Pine (*Pinus muricata*) was found, as has already been noted. This could only have been brought in by the tree mouse or some other animal. It will be remembered that Shelton (see page 141 above) noted a mouse traveling from tip to tip of the fir boughs, quickly escaping in a *Thuja plicata* which was the fourth tree from the nesting site. It is not improbable that the tree mouse ranges freely through the foliage of several trees in the vicinity of his home nest tree.

#### 8 HIBERNATION

Wilder suggests the possibility that the tree mice may hibernate in the cold region back from the coast, and records finding one in February, presumably at Carlotta, Humboldt County, California, curled up and dormant. The same day, however, he found two females with half grown young; so he concluded that the first must have been chilled into temporary inactivity by the storm just ended. Todd (1891, p. 242) suggests that the tree mice probably do not hibernate, on the basis of the tracks seen about the nest trees in the snow. But allusion has already been made to his uncertainty as to whether or not the tracks were those of *Phenacomys longicaudus*.

It is doubtful whether the cold weather is severe enough in the area of occurrence of *Phenacomys longicaudus* to make true hibernation necessary, although there may be inactivity during the colder periods. The writer has been unable to find any definite records of hibernation among the *Microti*, although Barrett-Hamilton and Hinton (1914, p. 466) refer to the inactivity during cold weather of *Microtus orcadensis sandayensis*. Bailey definitely asserts (1900, p. 6) that no American species of *Microtus* is known to hibernate.

## 9 STUDIES OF THE NEST

## (1) Altitude above the ground

The height of nests above the ground, varying as it does from four feet to one hundred feet, testifies to the freedom of movement of *Phenacomys longicaudus* in its arboreal habitat. Wilder writes that he has found several nests low enough in the trees to be reached from the ground. Shelton records the examination of a nest a hundred feet up. In Clay's experience eight and 100 feet are the extremes, with the prevailing height at 20 to 60 feet. Nests observed by our party ranged in altitude from eight to 60 feet.

## (2) Position in trees

A majority of the nests are located against or around the trunks of the trees. All those observed by Shelton in Oregon were situated next the trunk of the fir, where they were securely supported by one or more branches. Wilder asserts that in his experience most of the nests were located where several limbs join the trunk, although where nests have been found on large trees they have usually been near the ends of lower branches and at no great height above the ground.

Clay says that low nests are usually near the outer end of a drooping limb, but agrees that most nests are placed near the trunk of the tree.

All nests actually examined by our party at Mendocino City were built near the main trunk of the fir where a circlet of branches joined the tree, although we noted at least two nests on limbs several feet distant from the main trunk. In several instances the nest was built all around the trunk, so that the trunk actually traversed the center of the nest.

## (3) General size

Todd (1891, p. 241) says the nests are about the size of robins' nests, or even smaller. Shelton has examined a nest only eight or ten inches in diameter, the largest nest he has seen being about two feet in diameter by one in depth. Wilder asserts that when the nests are new they are about the size of a quart measure, old nests being larger, sometimes as large as a peck measure.

According to Clay the family nests were from nine to 12 inches in diameter in new structures, up to 30 inches or more across and 12 inches or more deep, in the older ones.

Nests observed by our party varied in dimensions from about 18 inches in length, breadth, and height to three feet in diameter and two or three feet in height, enormous structures when it is remembered that the maximum total length of the mouse is only about seven and one-half inches.

(4) Skeleton, form and makeup

(a) Possible parasitism of *Phenacomys longicaudus*

All nests observed by members of the Museum party in the vicinity of Hearst and Lierly's Ranch were apparently the appropriated nests of *Sciurus griseus griseus*, many of the sticks used in their construction being too large to have been carried by the tree mice. Shelton reports that he has found, in the course of his investigations in Oregon, only one nest of original *Phenacomys* construction, all others being old and remodeled nests of the gray squirrel.

All nests examined by us at Mendocino City, however, were probably built by tree mice exclusively, since there were no sticks used which were too large to be handled by them alone.

An interesting question arises as to the occupation of the gray squirrel's nests by *Phenacomys*. Does the tree mouse parasitize and finally drive out his larger arboreal neighbor, or does the mouse appropriate the nest only after its abandonment by the gray squirrel?

(b) Form and composition of the nests

Although one's first impression of those nests studied at Mendocino City was that they were loosely built, it was soon discovered that they were steadily fastened and rather difficult to dissect. Usually the structure was spherical in form with a slight flattening on top. Often the flattening was so pronounced as to make the nest hemispherical in form. The skeleton of the nests was formed entirely from twigs of the grand fir (*Abies grandis*). As used in the nest mass these twigs were dry and leafless. Making up a close interpacking was much material composed of the net-like fibrous mat of the net lichen, *Ramalina reticulata*, and of the resin ducts of fir leaves, the latter material predominating. Piled up above the thick mass of the main nest there was always a loose superstructure of twigs and branchlets. Some of these were of considerable size for the small mouse, the largest being one-eighth inch in diameter and four to eight inches long.

Residents told us that green twigs on the ground beneath the fir trees indicated not only the presence of a *Phenacomys* nest but also the fact that the nest was occupied. Although this would not seem always to be so, since we found green twigs under trees in which there were no nests, it would appear to be the rule. At any rate, green branchlets were noted on the ground under most of the occupied nests we investigated; and it was true in all instances where the nest was occupied that fresh green fir branchlets were pulled into the loose superstructure of dry twigs on top of the nest.

Reference has already been made to the fact that the nests found at Lierly's Ranch and Hearst, Mendocino County, were made up of sticks too large to be transported by *Phenacomys*, so doubtless originally constructed by the gray squirrel (*Sciurus griseus griseus*) or the wood rat (*Neotoma fuscipes fuscipes*). The lone individual tree mouse taken at Lierly's Ranch was found 50 feet up in a Douglas fir, in a nest 18 inches in diameter, built of sticks of fir and lined with "tree moss" (really the net lichen, *Ramalina reticulata*) which appeared to have been fluffed up by the occupants.

Our studies of nests at Mendocino City showed that below the level of the used portion of the nest there was usually found a mass of decaying matter, sweating and steaming like a pile of old manure or like green feed in a silo, a very large part of the nest being made up of this material. In composition this mass was nothing more than the resin ducts of fir leaves and net lichen with quantities of feces distributed through it. Occasionally, but not often, this old slowly decaying matter was relatively dry.

Well defined galleries traversed the nests in various directions, providing ready communication between the inner nest cavity and the outer world. When the nest was built all the way around the trunk of the tree a circular gallery, running around the trunk and communicating with runways leading to the nest cavity and the exterior, was usually found.

Bailey (1915, pp. 148-149) says some *Phenacomys* houses had only one nest [inner nest cavity], and others had as many as five. Concerning one nest examined by him he says: "The twigs of which it was largely composed had settled in a half decayed and earthy mass as solid as a muskrat's house, and

beginning at the top a tiny burrow wound down spirally through the structure to one after another of the four or five fresh, clean little nests of green spruce leaf fibers."

Shelton has described several nests studied by him in the vicinity of Eugene, Oregon. One nest, found approximately 100 feet above the ground in a Douglas fir on Spencer Butte, seven miles south of Eugene, was about two feet in diameter by one in depth. It was composed of dry twigs and moss and was beyond all doubt the nest of a gray squirrel (*Sciurus griseus*) remodeled for *Phenacomys* use. The exterior of the nest was wet and mouldy, but the interior was dry and warm. The inner nest was spherical in shape, about five inches in diameter, and composed of fir needle fibers. The nest cavity was within this ball-like structure, and communicated with the outside through a small round opening about an inch in diameter in the wall of the inner nest. A mouse, after traversing this opening, would find itself in the coarse outer structure of dry twigs and moss, through which escape was possible in any direction.

Another nest, found in February by Bovard and Shelton, was located 30 feet up in a Douglas fir. This was a large nest, doubtless originally belonging to a gray squirrel. Its coarse outer structure was of large dry twigs and moss. Within was a large quantity of fibrous material, apparently from the inner bark of the tree, and within this was the inner nest proper, a round ball of the characteristic shredded fibers of the fir leaves. The outer structure was wet and mouldy, and the entire nest was heaped high with piles of rotting feces. In this nest there were taken two young animals, half or two-thirds grown. In the course of the investigation, the nest was entirely dissected away, and there remained nothing of it. Returning to the same locality in June, another nest was found in practically the same crotch. This was a small nest, only eight or 10 inches in diameter, composed of soft moss and the fibers of the fir needles. A small quantity of feces had collected. As Shelton remarks, the indications are that the adult mice, returning and finding their home destroyed, had started a new one of their own construction. Incidentally it should be remarked that this was the only instance noted by Shelton of a nest of original *Phenacomys* construction.

Wilder writes that he has found mud-masses in some of the nests, and that the foundation of a fresh nest recently examined by him was of small dry branches and mud balls. In mentioning these facts, he suggests that possibly the nests containing mud are built upon structures started by some mud-mason like the robin, or possibly a wood rat, which makes use of anything loose it can find.

More extended reference is made below (see page 153) to the possibility of the existence of two kinds of nests, "male" nests and "family" nests. Clay has submitted the following description of the supposed nest of the male: "The male nest is a neat, compact, round ball of small twigs, five to eight inches in diameter or possibly a little larger, well lined with the usual material, containing one entrance hole as a rule, the opening facing the trunk of the tree and usually being well hidden by foliage. The favorite location is one where the fir needles are thickest on the limb, some distance away from the trunk of the tree. Annual additions were not in evidence in any of the male nests examined. Ordinarily only one nest is to be found in a tree, but in several instances in which the family tree was isolated the male's nest was found in the same tree with the family nest. The nest of the male is always higher in the tree than the family nest, and is usually well concealed."

(c) The inner nest cavity

All inner nest cavities examined by us were lined either with net lichen or with the fine fir-leaf resin ducts. In spite of the humidity of the surroundings and the dank character of the nest mass below it, this inner nest appeared to be dry and comfortable. The finely shredded character of the material used for the inner nest guarantees its softness, and the thickness of its walls probably insures a certain degree of heat in occupied nests. It is even possible that the slow oxidation of the nest-mass, as indicated by the sweating nature of the material beneath the occupied nest cavity, is a source of heat.

The cavity of the nest at Lierly's Ranch from which the tree mouse was secured was 10 inches across. It was always necessary to dissect away much outer material before the inner nest could be found. Located in the upper part of the nest as a whole, it was in all cases covered over and well protected from the outside.

Residents of Mendocino City said the tree mice lined their nests with hair, but this we failed to confirm.

As remarked above, feces were found in quantity throughout the entire nest structure, except in the inner nest cavities, although a few feces are present in a mass of inner nest cavity material which was saved and brought to the Museum.

Even this much of a localization in the deposition of excrement is interesting, as it seems to indicate an early stage in the development of an instinct of sanitation.

(5) Large nests the work of years

Observations have already been made concerning the extremes of size displayed by different nests. For example, Todd records noting a structure the size of a robin's nest (1891, p. 241), or even smaller (in True, 1891, p. 304). Our party observed nests which were as much as two or three feet in height and three feet in transverse diameter. A significant point regarding these larger nests is that only their upper portions were in use.

Clay reports that the family nests showed signs of being renewed at least annually and possibly at even more frequent intervals. Deserted beds were found under or alongside those which were occupied. The type of branching at the point where the nest was located was a most important factor in determining the form of the nest. Some nests were built wide; in these the deserted inner cavities would be on a level with the occupied one. Others were built high rather than wide; in these the deserted beds would be superimposed one above the other. It seems clear that each nest becomes larger year by year. Apparently the discarded resin ducts of the fir leaves with the twigs remaining after the tree mouse has eaten off the fleshy portions of the leaves are immediately incorporated into the nest mass. This, in itself, would cause a continuous increase in size. Whether there is a new nest actually built on top of the old mass every year is unknown, but it is not improbable that some such regular addition is constructed.

(6) Desertion of nests

Under this head Todd (1891, p. 241) says: "For some reason which I have not been able to discover, these nests seem to be frequently changed or deserted, from the fact that



we frequently find in the woods and under lone trees of this variety, on the ground, small parts and at times almost, as it appears, the entire nest." Wilder says that the tree mouse seems to desert nests which have been disturbed, and has found a few nests apparently permanently unoccupied. Nearly all the nests examined by our party at Lierly's Ranch and at Hearst were apparently deserted or unoccupied. Animals were actually taken in eight out of 13 nests we carefully investigated at Mendocino City. Of the five nests we found to be unoccupied, some were doubtless deserted, while the dwellers in the others may have been out at the time of our visits.

Wilder has often noticed the disappearance of entire nests previously located. This together with Todd's record of finding portions of nests on the ground clearly indicates the presence of enemies of the tree mouse. Doubtless the small boy is at present the chief of these.\* Although there is nothing definite on this head Mr. Wilder suggests cats and horned owls as possible additional enemies. There is a possibility also that unusual gales of wind may occasionally dislodge the nests.

#### 10 BREEDING HABITS AND FAMILY RELATIONS

##### (1) Time of breeding and size of families

On July 15 and 17 we found young in three nests at Mendocino City. In each of two cases, there were two young, in one case a single individual. Shelton took two young from a nest at Spencer Butte, near Eugene, Oregon, on February 21. Wilder found a female and two half grown young in Humboldt County, California, during the same month, and asserts that the tree mice seem to breed all through the spring and summer. Clay opened four nests containing three young each, and says the breeding season seems to occur from the middle of April till late in the summer.

It may be that, like some species of *Microtus*, the young may be born at any season, but it is perhaps more probable that their birth is limited to late winter, spring and summer. Two pairs of abdominal mammæ are borne by the females, which indicates that litters are small.

The young are evidently helpless for some days after being born, remaining for the time in the inner nest cavity. Young in three out of the four nests investigated by Clay had not yet opened their eyes.

## (2) Preponderance of females

Of all the sexed specimens of *Phenacomys* available 10 are males and 20 females. This preponderance of the females in series of *longicaudus* is impressive, and the question immediately arises, why should there be such a discrepancy in numbers of the sexes?

Segregating the specimens according to age, we find that of the eight adults, their age being determined on the basis of the degree of emergence of their cheek teeth, only two are males.

Twelve specimens of *Phenacomys orophilus* are equally divided between the sexes, there being six of each. Of four fully adult *orophilus*, one is a female and three males.

There are at least two possibilities to be considered: (1) that the mice are polygamous or promiscuous, and that there are actually more females than males; (2) that the female adults remain more closely in the nests than the males do, and are taken in greater numbers by our methods of capture, which involved the dissection of the nests.

It may be that both these possibilities are effective. Of the eight youngest examples at hand six are males and two females, but of all the young of *longicaudus* available, eliminating four alcoholics not sexed, eight are males and thirteen females. It appears that among the young individuals the proportion of females to males is well below two to one, while among the adults the proportion is four to one.\* If males and females are born in equal numbers the young, supposedly non-breeding individuals, should have divided up equally between the sexes. But since they did not, one is tempted to the conclusion that females are actually about twice as numerous as males.

On the other hand, the difference in proportions of females to males in the series of young and adults respectively seems to indicate that the females do remain more closely in the nests than the males and so were taken in greater numbers by the methods of capture employed.

*Orophilus* and *albipes*, being taken by free trapping on the ground, would probably not give the bias in the number of

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\*The classification of the specimens into adult and young is an arbitrary one, and several of the examples classed as young probably are breeders.

females that the dissection of the nest would. In fact, since the males may be more active as foragers than the females, there might even be a disproportion of males.

### (3) Family relations

In each nest in which young were discovered there was one inner nest cavity and one brood of young. This would seem to indicate that only one family lives in each occupied nest. Possible evidence to the contrary was the capture of two seemingly adult males in a tree in which a nest was being dissected. It is not certain, however, that both these mice came from this nest.

Wilder says that he has several times found the female and young in a large nest, and the male in a small nest a few feet higher in the same tree. After remarking upon the difficulty he has had in finding males he suggests that it is possible they live in nests separate from those of the females, in the large trees, where their small nests would not be noticed, while the females for the most part select smaller trees.

Clay asserts that the male and female of a family do not live in the same nest during the rearing of the young, although it is probable that the males do seek the family nest thereafter. The small nest of the males would be likely, says he, to be destroyed by storms, necessitating the building of a new nest each season. On January 6, 1912, two adults were found in one nest, the one secured being a female. Clay suggests that the "escape" was a male, and that the incident would support the theory that the male and female live together during the winter months.

This most interesting suggestion of Wilder and Clay deserves further investigation. If it is in accord with the facts, there would be furnished an additional reason for the preponderance of females in our series; for the large family nests would be much more likely to be dissected than the small nests of the males. It seems to the writer that the evidence on this point of the separate nests for the sexes is inconclusive.

E THE POSSIBLE ANCESTRY OF *PHENACOMYS*  
*LONGICAUDUS* TRUE

The known characters and distribution of the members of the genus would seem to support the theory that the subgenus *Arborimus* is derived from the subgenus *Phenacomys*, or that both subgenera are derived from a common ancestral stock not very different from either; and that the isolation of portions of the parent stock was an important factor in their differentiation.

It is furthermore possible if not probable that both *Phenacomys longicaudus* and *Phenacomys albipes* are descended from the same species, doubtless a member of the subgenus *Phenacomys*. Compared with *albipes*, *longicaudus* would seem to be a little more specialized. The two species may exemplify successive migrations of similar individuals from a common center, *longicaudus* being of the first wave, *albipes* of the second. *Longicaudus* would in this way have had time to become more specialized than *albipes*.

It is almost impossible to avoid the inference that the long tail in *Phenacomys longicaudus* and the arboreal habit are in some way associated.

Allen has recently shown (Bull. Amer. Mus. Nat. Hist., 34, 1915, p. 166) that the tail in different groups of tree squirrels is developed in proportion to their exclusiveness as tree dwellers, the ratio of tail length to total length varying in the different groups from about 40 to 52 per cent. Ground-living species of *Phenacomys* (except *albipes*) have ratios of 25 per cent, *albipes* (ground living) has an average ratio of 38 per cent, and *longicaudus* (tree dwelling) of approximately 40 per cent.

As implied above, it seems certain, from the close general similarity between the tree mouse and its ground living relatives, that the long-tailed arboreal species is derived from some short-tailed terrestrial form.

The possible connection between the long tail of *P. longicaudus* and its arboreal habitat suggests a train of puzzling questions.

Did *P. longicaudus* acquire its long tail and then take to the trees? Or did it take to the trees and then gradually

acquire its long tail? If it got its long tail while still living on the ground, taking to the trees when the tail reached approximately its present length, why has not *P. albipes*, which has a tail nearly as long, also adopted an arboreal habitat? If *Phenacomys longicaudus* took to tree life while still short-tailed, acquiring its long appendage thereafter through some form of environmental or other pressure associated with arboreal life, how is the acquisition of a long tail by the wholly ground-living *P. albipes* to be explained?

But in this connection it ought to be remembered that, in view of the small number of specimens of the latter species which have been taken, and of our ignorance concerning its life history, we are hardly in a position to state positively just where its habitat does lie.

Perhaps the ancestor of both *longicaudus* and *albipes* was long-tailed and is extinct and unknown. In this case possibly *longicaudus* merely selected the arboreal habitat for which its characters already fitted it. There remains the problem of why the similar *albipes*, which is to all appearances equally well fitted for tree life, did not also become a tree mouse.

If *longicaudus* and *albipes* represent successive waves of migration, perhaps *longicaudus* may be conceived to have attained to the arboreal environment before the development of *albipes*. If this were so the prior occupancy of the tree habitat by *longicaudus* would possibly be sufficient to account for the terrestrial predilections of *albipes*.

It should here be noted that if the hypothesis is true, that *Phenacomys longicaudus* is derived from some ground-living microtine, we have presented in the phylogeny of the tree mouse an unusual type of migration. The writer has already emphasized (The status of the beavers of western North America, Univ. Calif. Publ. Zool., vol. 12, in press) that in general each group of mammals occupies the same ecologic niche in different places rather than different ecologic niches in the same place. The *Microtinae* are characteristically terrestrial, with some members adapted to a more or less aquatic, and others to a more or less fossorial, mode of life. Apparently the stock which we now know as *Phenacomys longicaudus*, in the course of its phylogeny, has broken away from the time-honored group niche in which all other members of its subfamily

are found, and has come to occupy a niche entirely different. It has performed not only the usual geographic migration, but also the comparatively rare ecological migration.

## F SUMMARY

1. For 22 years subsequent to its discovery the microtine rodent *Phenacomys longicaudus* True was represented in natural history museums by but three specimens. There have been recent accessions of notes and specimens which permit of substantial contributions to knowledge of its systematic and ecologic status.

2. Habits and associational relations are just as much a part of the animal as its physical characters. In the interest of adequacy and comprehensiveness, emphasis upon study in these fields should and probably will become more insistent as time goes on.

3. *Phenacomys longicaudus* is the type of *Arborimus*, a new subgenus of *Phenacomys*. The most striking characters of the type are its cinnamon reddish dorsal coloration, its long tail, and its arboreal habitat.

4. *Phenacomys albipes* Merriam is tentatively referred to the new subgenus, though it is intermediate in certain characters between *Arborimus* and *Phenacomys*, and differs from *P. longicaudus* in several important particulars.

5. The subgenus *Arborimus* is restricted to the humid coast belt of western North America, specimens having been taken in southwestern Oregon and northwestern California only.

6. All the clear evidence at hand indicates that the tree mouse is dependent on the trees in which it lives for food, drink and shelter.

7. The tree mouse has been found nesting in the Sitka spruce (*Picea sitchensis*), the grand fir or lowland fir (*Abies grandis*), and the Douglas fir (*Pseudotsuga taxifolia*).

8. Ordinarily the nests are found in groups, so that it is proper to refer to the animal as loosely colonial.

9. Our experience with *Phenacomys longicaudus* did not show it to possess any extraordinary agility, quickness, or aggressiveness.

10. The tree mouse, from all evidence, feeds principally

on the fleshy portions of the fir needles and the cortical portions of young fir shoots, leaving the resin ducts and stripped shoots to be incorporated into the nest structure.

11. It seems probable that each individual tree mouse ranges freely through the foliage of several trees in the vicinity of its home nest-tree.

12. Probably *Phenacomys* does not hibernate, though it may become less active or altogether inactive during the coldest weather.

13. The nests vary much in size and in altitude above the ground. A majority are built against or near the trunks of the trees. In some localities old gray squirrel nests have been occupied by the tree mice. All nests examined at Mendocino City were apparently of original *Phenacomys* construction. Twigs, branchlets, resin ducts of fir leaves, and net lichen (*Ramalina reticulata*) were the chief materials used. The inner nest cavity was of soft material, either the resin ducts of fir leaves or tree moss. The nests increase in size with age; whether the increment is due to gradual accumulation of material or to annual additions at some particular season is unknown. Some of the nests seem to have been deserted.

14. Young have been found in the nest in February and in July. Numbers of young actually taken were three per family in four instances, two per family in four additional instances, and one in a single case.

15. The number of females in our collections is disproportionately large. It is possible that females are actually more numerous than males, and also that our methods of capture, involving the destruction of nests, have resulted in a larger number of females being taken.

16. Apparently only one family occupies a nest.

17. There is evidence which seems to show that males live in nests separate from those of the females for at least a part of the year, the male nests being smaller and different in other respects from the family nests; but the data are as yet incomplete and inconclusive.

18. Probably *Phenacomys longicaudus* and *P. albipes* are derived from the same species, doubtless a member, past or present, of the subgenus *Phenacomys*. Several interesting questions regarding the characters of *longicaudus* and *albipes* and their relation to habits and environment await answer.

G LIST OF WORKS CONTAINING IMPORTANT  
MATERIAL RELATIVE TO THE GENUS  
*PHENACOMYS*

## ALLEN, J. A.

1894. Descriptions of ten new North American mammals, and remarks on others. Bull. Amer. Mus. Nat. Hist., 6, 331-332.  
Original description of *P. truei* (= *P. orophilus*).
1894. Recent progress in the study of North American mammals. Author's ed., extracted from Abstract Proc. Linn. Soc. New York for year ending March 27, 1894, pp. 1-29 (17 to 45 in original form).  
Notes description of genus *Phenacomys* by C. H. Merriam, and lists six forms; contains note on origin and distribution (p. 15 = p. 31 original).
1899. On mammals from the Northwest Territory collected by Mr. A. J. Stone. Bull. Amer. Mus. Nat. Hist., 12, 1-9.  
Original description of *P. constablei* (p. 4).

## ANDERSON, E. M.

1915. Revised list of mammals collected in the Okanagan Valley in 1913. Province of British Columbia, Report of the Provincial Museum of Natural History for the year 1914, pp. 20-21.  
Record of capture of *P. orophilus* at Schoonover Mountain (Okanagan Falls), British Columbia (p. 20).

## BAILEY, V.

1915. Discovery of the tree mouse (*Phenacomys longicaudus* True). Oregon Sportsman, 3, 147-149.  
Valuable article on habits.

## BANGS, O.

1900. Three new rodents from southern Labrador. Proc. New Eng. Zool. Club, 2, 35-41.  
Original description of *P. celatus crassus* (p. 39).

## BARRETT-HAMILTON, G. E. H., and HINTON, M. A. C.

1914. A history of British mammals. (London, Gurney and Jackson) Pt. XVI, November 1914, pp. 457-504, pls. 2 full-page colored, and black and white, figs. in text 73-84.  
Fossil material erroneously referred to *Phenacomys* by Nehring disposed in the genus *Mimomys* Forsyth Major (p. 473 footnote).

## CARY, M.

1911. A biological survey of Colorado. U. S. Dept. Agric., Bureau Biol. Survey, N. Amer. Fauna, 33, 256 pp., 12 pls., 39 figs. in text.  
Lists two species of *Phenacomys* from Colorado, giving full treatment to each (pp. 119-120).

## ELLIOT, D. G.

- 1899a. Preliminary descriptions of new rodents from the Olympic Mountains. Field Columb. Mus., Zool. Ser., 1, 225-226.  
Original description of *P. olympicus*.
- 1899b. Catalogue of mammals from the Olympic Mountains, Washington, with descriptions of new species. Field Columb. Mus., Zool. Ser., 1, 239-276, pls. XLI-LXI, unnumb. figs. in text.  
Habitat, characters, and abundance of *P. olympicus* (p. 255).



1901. A synopsis of the mammals of North America and the adjacent seas. Field Columb. Mus., Zool. Ser., 2, xiv + 471, 49 pls., 94 figs. in text.  
Seven species of *Phenacomys* listed from North America (pp. 167-169).
1905. A check-list of mammals of the North American continent, the West Indies and the neighboring seas. Field Columb. Mus., Zool. Ser., 6, v + 761, frontispiece.  
Recognizes ten forms of *Phenacomys* (pp. 226-228).
1907. A catalogue of the collection of mammals in the Field Columbian Museum. Field Columb. Mus., Zool. Ser., 8, viii + 694, 92 figs. in text.  
Specimens of the following are in Museum: *P. orophilus*, *P. olympicus* (p. 282).
- FLOWER, W. H., and LYDEKKER, R.
1891. An introduction to the study of mammals living and extinct. (London, Adam and Charles Black), xvi + 763, 357 figs. in text.  
Two-line general reference to the genus *Phenacomys* (p. 466).
- GRINNELL, J.
1913. A distributional list of the mammals of California. Proc. Calif. Acad. Sci., Ser. 4, 3, 265-390, pls. 15, 16.  
Lists three forms of *Phenacomys* from California (pp. 315-316).
- HOLLISTER, N.
1912. Mammals of the Alpine Club Expedition to the Mount Robson region. Canadian Alpine Journal, Special Number, 1-44, 13 pls.  
Treats *P. intermedius*; suggests that *P. orophilus* is identical with or only slightly differentiated from *P. intermedius* (pp. 20-21).
- JEWETT, S. G.
1915. Discovery of a rare rodent. Oregon Sportsman, 3, 37-38.  
Record of capture of second known specimen of *P. albipes* on McKenzie River, Lane County, Oregon.
- LYDEKKER, R.
1896. A geographical history of mammals. (Cambridge, University Press) xxi + 400, map, 82 figs. in text.  
Three-line general reference to genus *Phenacomys* (p. 342).
- LYON, M. W., JR., and OSGOOD, W. H.
1909. Catalogue of the type specimens of mammals in the United States National Museum, including the Biological Survey collection. U. S. Nat. Mus., Bull. 62, x + 325.  
Types of six described species of *Phenacomys* are in the government collections (pp. 96, 97).
- MERRIAM, C. H.
1889. Description of a new genus (*Phenacomys*) and four new species of Arvicolinæ. U. S. Dept. Agric., Div. Ornith. and Mamm., N. Amer. Fauna, 2, 27-35, 5 pls., 3 figs. in text.  
Original description of the genus, as well as of *P. intermedius*, *celatus*, *latimanus*, and *ungava*.

1891. Results of a biological reconnoissance of south-central Idaho. U. S. Dept. Agric., Div. Ornith. and Mamm., N. Amer. Fauna, 5, vii + 113, pls. 4, 4 figs. in text.  
Original description of *P. orophilus* (pp. 65, 66).
1892. The geographic distribution of life in North America with special reference to the Mammalia. Proc. Biol. Soc. Wash., 7, 1-64.  
Seven species of *Phenacomys* listed (p. 25).
1897. *Phenacomys preblei*, a new vole from the mountains of Colorado. Proc. Biol. Soc. Wash., 11, 45.  
Original description of *P. preblei*.
1899. Results of a biological survey of Mount Shasta, California. U. S. Dept. Agric., Div. Biol. Surv., N. Amer. Fauna, 16, 179 pp., pls. 5, 46 figs. in text.  
*P. orophilus* recorded from Squaw Creek, Mount Shasta (p. 95).
1901. Two new rodents from northwestern California. Proc. Biol. Soc. Wash., 14, 125-126.  
Original description of *P. albipes*.

## MILLER, G. S., JR.

1896. Genera and subgenera of voles and lemmings. U. S. Dept. Agric., Div. Ornith. and Mamm., N. Amer. Fauna, 12, 1-84, pls. 3, 40 figs. in text.  
Genus *Phenacomys* (pp. 40-42).
- 1897a. Synopsis of the voles of the genus *Phenacomys*. Proc. Biol. Soc. Wash., 11, 77-87.  
General statement, characterization of genus, key to species, accounts of status, characters and distribution of six forms of *Phenacomys*. *P. truei* and *P. oramontis* are referred to *P. orophilus*. *P. celatus* is referred to *P. ungava*. A bibliography of the genus, containing fourteen titles, is appended.
- 1897b. Notes on the mammals of Ontario. Proc. Bost. Soc. Nat. Hist., 28, 1-44.  
Records capture of seven specimens of *P. latimanus* at Peninsula Harbor, Lake Superior; discusses characteristics and habits (pp. 8, 19-22).
1912. List of North American land mammals in the United States National Museum, 1911. Bull. U. S. Nat. Mus., 79, xiv + 455.  
Lists eleven species of *Phenacomys*. *P. truei* is referred to *P. orophilus*; and *P. celatus* to *P. ungava* (pp. 208, 209).

## MILLER, G. S., JR., and REHN, J. A. G.

1901. Systematic results of the study of North American land mammals to the close of the year 1900. Proc. Bost. Soc. Nat. Hist., 30, 1-352.  
Lists nine forms of *Phenacomys* from North America (pp. 111-112).
1903. Systematic results of the study of North American land mammals during the years 1901 and 1902. Proc. Bost. Soc. Nat. Hist., 31, 61-145.  
Notes two species of *Phenacomys* added to the list since their contribution in 1901 (p. 90).

PALMER, T. S.

1904. Index generum mammalium: a list of the genera and families of mammals. U. S. Dept. Agric., Div. Biol. Surv., N. Amer. Fauna, 23, pp. 984.  
Reference to *Phenacomys* (p. 531).

PREBLE, E. A.

1902. Descriptions of new species of *Synaptomys* and *Phenacomys* from MacKenzie, Canada. Proc. Biol. Soc. Wash., 15, 181-182.  
Original description of *P. mackenzii*.

RHOADS, S. N.

1895. Additions to the mammal fauna of British Columbia. Amer. Nat., 29, 940-942.  
Original description of *P. oramontis* (= *P. orophilus*).

SETON, E. T.

1909. The life histories of northern animals, an account of the mammals of Manitoba (New York City, Charles Scribner's Sons), 1, xxx + 673, 46 pls., 38 maps, 182 figs. in text.  
General reference to the genus *Phenacomys*, with fragmentary diagnosis (p. 516).

STEPHENS, F.

1906. California mammals. (San Diego, West Coast Publishing Co.), 351 pp., frontispiece, many unnumbered figs. in text.  
Lists two species of *Phenacomys* from California (p. 123).

STONE, W.

1904. On a collection of birds and mammals from Mt. Sanhedrin, California (with field notes by A. S. Bunnell). Proc. Acad. Nat. Sci. Phila., 1904, 576-583.  
Record of finding specimen of *P. longicaudus* dead in road near "Lierlie's" Ranch, June 30, 1899 (p. 578).

TAYLOR, W. P.

1915. Relative numbers in sexes of the tree mouse. Oregon Sportsman, 3, 150-151.  
Incorporated in present paper, pp. 152 to 153.

TODD, A.

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Habits and probable distribution of *P. longicaudus*.

TROUESSART, E. L.

1897. Catalogus mammalium tam viventium quam fossilium. (Berolini, R. Friedländer und Sohn), fasc. III, 453-664.  
Lists six species of *Phenacomys* (pp. 547-548).

TRUE, F. W.

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Original description of *P. longicaudus*.

WARREN, E. R.

1912. Notes on the distribution of some Colorado mammals. Proc. Biol. Soc. Wash., 25, 1912, 3-8.  
Additional record of *P. orophilus* in Colorado (p. 4).